

## Cenozoic *Nacella* (Patellogastropoda: Nacellidae) from Peru and Chile: Filling in the Gaps

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**Abstract.** The limpet genus, *Nacella* Schumacher, 1817 (Patellogastropoda: Nacellidae), is noted for its adaptation to cold water at high austral latitudes. The finding of at least five new Pliocene species (*Nacella* (*Nacella*) *lacrima*, sp. nov.; *N. (Patinigera) oblea*, sp. nov.; *N. (Patinigera) chalaensis*, sp. nov.; *N. (Patinigera) intiforma*, sp. nov.; and *N. (Patinigera) oconaensis*, sp. nov.) and one new late Oligocene species (*N. (Patinigera) reicheae*, sp. nov.) from tropical latitudes of southern Peru, as well as the recognition of the southern Chilean *N. (Patinigera) nielseni*, sp. nov., newly named and reassigned to the late early Miocene, demonstrates the ecological range of *Nacella* once overlapped that of its warm-water sister genus, *Cellana* H. Adams, 1869. While determining the time and place of *Nacella*'s origin awaits the discovery of additional fossils, those found so far show modern sub-Antarctic *Nacella* taxa may have had low-latitude ancestors.

### INTRODUCTION

The patellogastropod genus, *Nacella* Schumacher, 1817, is comprised almost entirely of limpets living at high southern latitudes (Powell, 1973), including several taxa from southern Chile and Argentina (Valdovinos & R uth, 2005). Just one extant South American species, the Chilean *N. (Patinigera) clypeator* (Lesson, 1831), ranges into warmer waters of the southeastern Pacific Ocean (Ram rez-B hme, 1996; Valdovinos & R uth, 2005; V. Mogollon, written communication, 2008), as it did, too, during the Pleistocene (Herm, 1969). Other fossil Quaternary *Nacella* include the extant *N. (Patinigera) deaurata* (Gmelin, 1791) and *N. (Patinigera) magellanica* (Gmelin, 1791) from Patagonia, Argentina (Aguirre et al., 2005, 2006). Reported Pliocene examples of *Nacella* include *N. (Patinigera)* cf. *N. concinna* (Strebel, 1908) from lower upper Pliocene basaltic conglomerates on Cockburn Island, Antarctic Peninsula (Jonkers, 1988; Jonkers & Kelley, 1998) and *N. (Patinigera)* aff. *N. terroris* (Filhol, 1880) from coarse-grained sandstones of Chilo , southern Chile (Watters & Fleming, 1972). A doubtful account exists of Miocene *N. deaurata* from Patagonia (Brunet, 1997), where mollusks from Quaternary marine terraces are interspersed among older Tertiary taxa of the Entrerriense Formation.

Molecular phylogenetic studies show extant *Nacella* to be a paraphyletic grade or monophyletic clade most closely related to a clade encompassing extant species of *Cellana* H. Adams, 1869 (Koufopanou, 1999; Harasewych & McArthur, 2000; Nakano & Ozawa,

2007; Yoon & Kim, 2007). *Cellana* presently ranges throughout the tropical Indo-Pacific region, with species also found in Japan, Australia, New Zealand and on the Juan Fernandez Islands, 700 kilometers west of Chile (Powell, 1973). Fossil *Cellana* have been reported from South Africa (Pliocene: Kensley, 1972), Australia and New Zealand (late Eocene, early Miocene, and Pliocene-Pleistocene: Powell, 1973; Beu & Maxwell, 1990), the Antarctic Peninsula (late Eocene: Stillwell & Zinsmeister, 1992), and Chile (Pliocene: Herm, 1969). An Early Cretaceous record from Australia, *Cellana carpentariana* Skwarko, 1966 (*vide* Powell, 1973), remains unconfirmed. The oldest *Cellana* verified on the basis of shell microstructure is the late Eocene *C. ampla* Lindberg & Hickman, 1986, from Oregon. The timing and place of the *Nacella-Cellana* evolutionary split and the reasons for the Recent disjunct distribution of *Cellana* (mostly tropical, Indo-Pacific) and *Nacella* (mostly cold-water, Southern Ocean) are still disputed (Koufopanou et al., 1999; Goldstien et al., 2006; Nakano & Ozawa, 2007).

This paper fills biogeographical and temporal gaps in the history of *Nacella* with the description of five new Pliocene species from tropical latitudes of southern Peru: *N. (Nacella) lacrima*, sp. nov.; *N. (Patinigera) oblea*, sp. nov.; *N. (Patinigera) chalaensis*, sp. nov.; *N. (Patinigera) intiforma*, sp. nov.; and *N. (Patinigera) oconaensis*, sp. nov. The Pliocene nacellid from Chilo  is reassigned a late early Miocene age and formally named *N. (Patinigera) nielseni*, sp. nov. *Nacella (Patinigera) reicheae*, sp. nov., from uppermost Oligocene beds of southern Peru, ranks as the oldest known *Nacella*. The newly established longevity of *Nacella*

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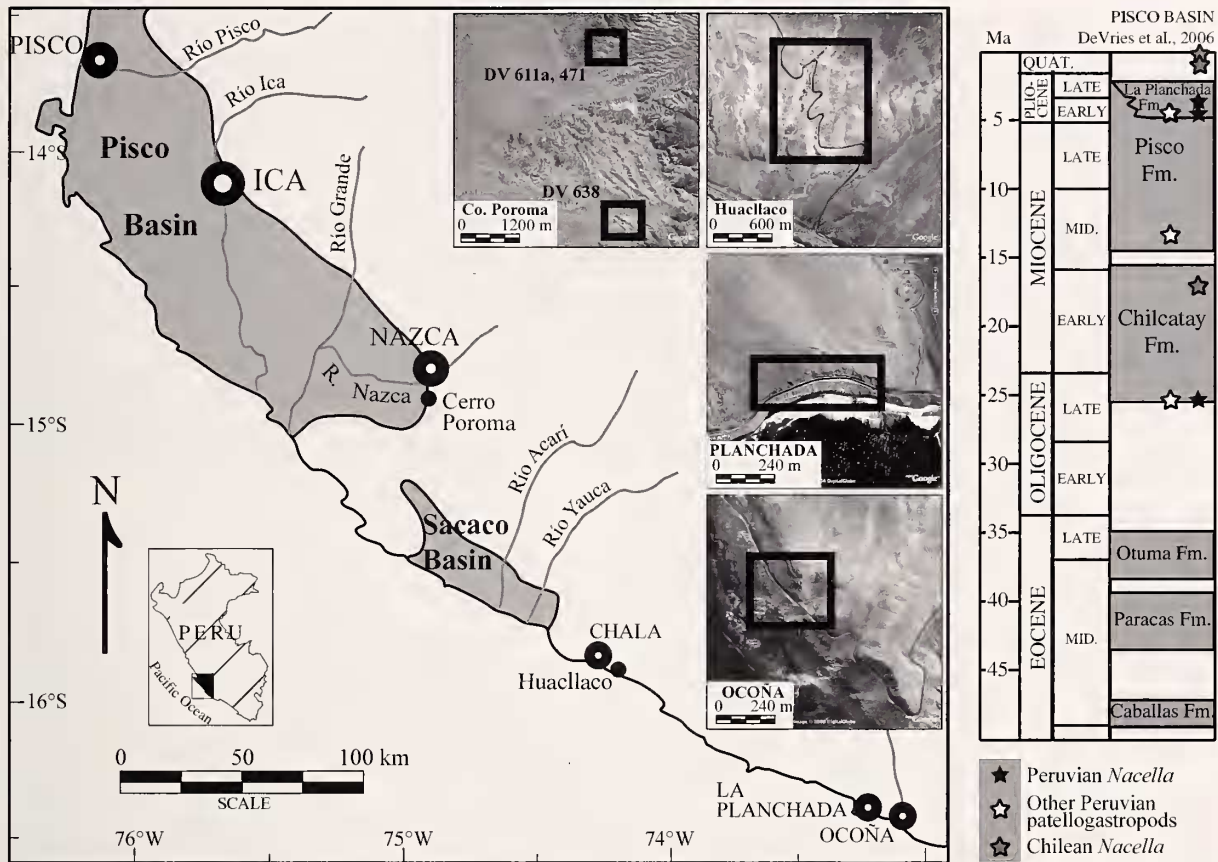


Figure 1. Location and Cenozoic stratigraphy of the Cenozoic Pisco and Sacaco forearc basins in southern Peru and type or other significant localities with *Nacella* specimens. Ocoña: type locality-sample (DV 1279-1) of *Nacella (Nacella) lacrima*, sp. nov., *N. (Patinigera) intiforma*, sp. nov., and *N. (Patinigera) ocoñaensis*, sp. nov. La Planchada: locality-sample DV 1267-1, with *N. (Patinigera) intiforma*. Huacllaco: type locality-sample (DV 1254-2, DV 1254-bal6) of *N. (Patinigera) oblea*, sp. nov. and (DV 1628-1) *N. (Patinigera) chalaensis*, sp. nov. Cerro Poroma: type locality-sample (DV 611a-1) and locality-samples DV 471-1 and DV 638-1 with *N. (Patinigera) reicheae*, sp. nov. Road visible in each inset is the Pan-American Highway; images from Google Earth. Locality details are in the Appendix. Stratigraphic column shows temporal distribution of South American patellogastropods, including *Nacella* from Peru and Chile.

helps refine scenarios for its origin, while its low-latitude diversity challenges our understanding of the biogeographical constraints on its modern distribution.

### GEOLOGY

The Cenozoic stratigraphy of southern Peruvian forearc basins was reviewed by DeVries (1998). *Nacella*-bearing beds were encountered at Cerro Poroma, near Nazca (Figures 1, 2F), where upper Oligocene bioclastic sandstone and conglomerate of the Chilcatay Formation overlap an Eocene peneplain, and farther south in the Pliocene La Planchada Formation, which is composed of baland coquina, bioclastic conglomerate, coarse-grained bioclastic sandstone, and fine-bedded gravel (Beudet et al., 1976), the remnants of littoral deposits dropped at the foot of steep sea cliffs.

Three outcrops of the La Planchada Formation along the Pan-American Highway deserve mention. A 70-meter measured section at Huacllaco (Figure 1) contains inferred upper lower Pliocene (Unit I) and upper Pliocene (Units II, III) bioclastic sediments capped by the most elevated and oldest marine terrace (Unit IV, uppermost Pliocene) (DeVries, 2003). Specimens of *Nacella* occur throughout the section, as do *Fissurella* and other littoral invertebrates that lived on rocky substrates (DeVries, 2003, 2006, 2007, 2008).

A second outcrop occurs in a quarry near Ocoña (Figure 1). The base consists of scour-bound lenses of angular boulders. Some lenses lack evidence of marine influence, but others have boulders encrusted with barnacles and oysters (Figure 2D). The rocky lenses are overlain with rippled and thin-bedded coarse-grained sandstone (Figures 2A, 2B) with scour-and-fill structures, imbricate slate pebbles, and ash laminae sur-



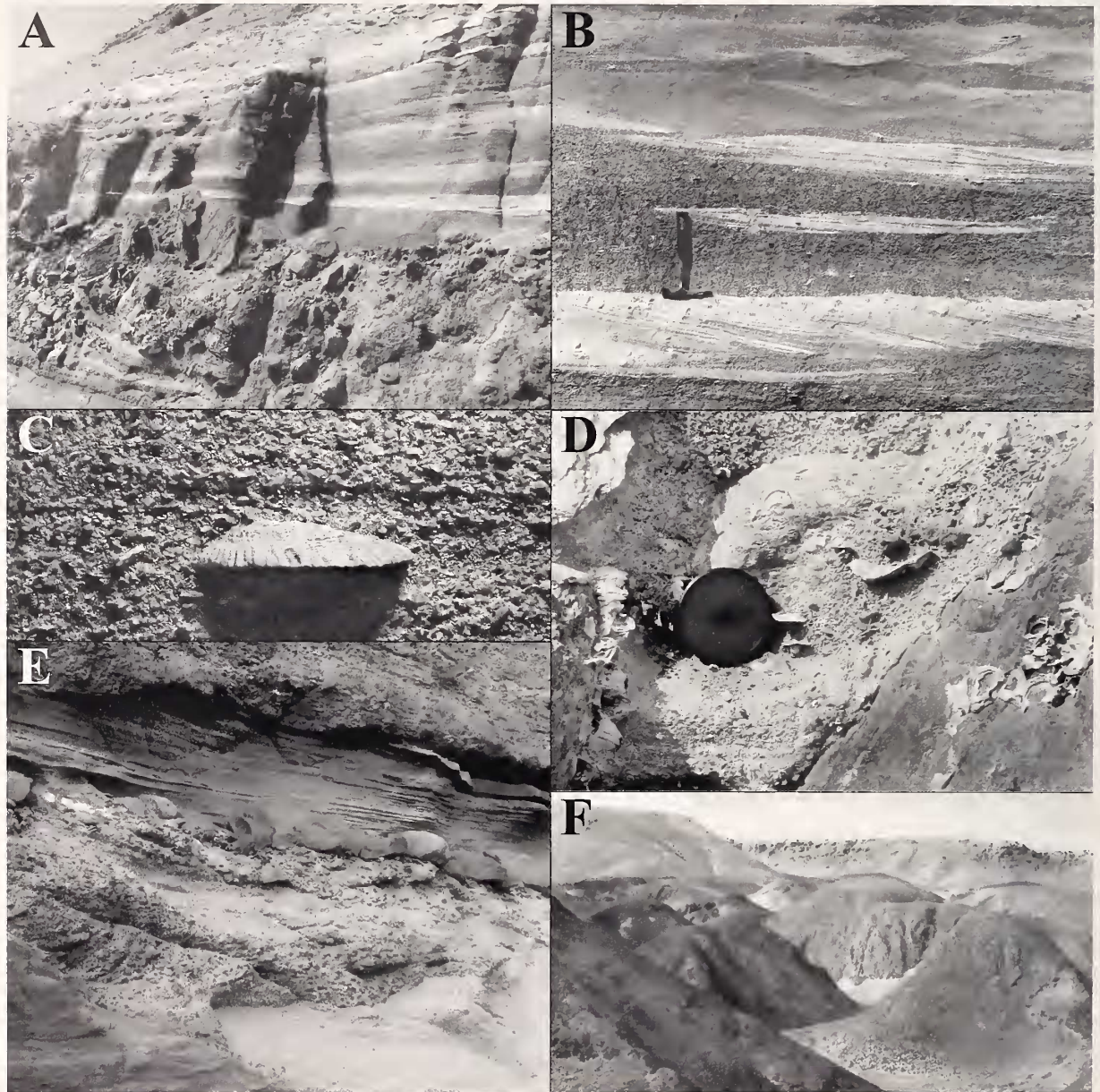


Figure 2. *Nacella* localities in southern Peru. A. Ocoña: interbedded rock-fall alluvium and finely bedded, tuffaceous, *Nacella*-bearing gravel and coarse-grained sandstone. B. Ocoña: cross-bedded and rippled tuffaceous gravel and sandstone containing *N. lacrima*, *N. intiforma*, and *N. oconaensis*. Shoreline is to left. C. Ocoña: close-up of *N. intiforma*, sp. nov., in fine-grained gravel. D. Ocoña: Debris-flow conglomerate with boulders encrusted with barnacles (left) and oysters (right). E. La Planchada: Finely bedded *Nacella*-bearing gravel, lowest left; early Pliocene cross-bedded bioclastic conglomerate, lowermost left-most set; Pleistocene cross-bedded bioclastic conglomerate, center; laminated sandstone and continental alluvium, upper left and right. F. Cerro Poroma: Post-Incaic granitic peneplain dissected by late Oligocene and modern erosional fissures, with continental volcanoclastics of early Miocene Nazca Group in background. Marine conglomerates with *Nacella reicheae*, sp. nov., occur in shallow fissures and at base of sedimentary sequence.

rounding small basement paleo-stacks, features that indicate a low-energy paleoenvironment in an otherwise high-energy setting, perhaps below wave base adjacent to steep sea cliffs (but see Cantalamessa & Di Celma (2005) for an interpretation of texturally

contrasting Chilean strata as paleotsunami deposits). Bedded marine deposits grade upwards into boulder-choked alluvium. The thin-bedded sandstone contains disarticulated flat-lying bioclasts of *Ostrea*, *Chlamys*, and *Nacella* (Figure 2C). A late early Pliocene age is

inferred from correlations with outcrops near Sacaco having age-diagnostic molluscan taxa (Muizon & DeVries, 1985; DeVries, 2003).

The third Pliocene *Nacella*-bearing outcrop is exposed south of La Planchada (Figures 1, 2E). The lithology and sedimentary textures are similar to those at Ocoña. The fauna consists of beds of disarticulated *Ostrea* valves, rare *Chlamys* valves, barnacles, and *Nacella*.

## MATERIALS AND METHODS

Specimens of fossil Peruvian *Nacella* described in this study were found by the author unless noted otherwise. Examples of extant species of the patellogastropod genera *Lottia* Sowerby, 1834, *Cellana*, and *Scurria* Gray, 1847, were available for comparison. References to modern sea surface temperatures (SSTs) in western South America are based on the World Ocean Atlas 2005 (Locarnini et al., 2006).

Locality and sample descriptions are listed in the appendix. Lengths (L), widths (W), and heights (H) are measured in millimeters. Dimensions of broken specimens are enclosed by parentheses. Most figured specimens are coated with ammonium chloride. Types and other numbered specimens are deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM) and the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Peru (MUSM INV).

## SYSTEMATIC PALEONTOLOGY

### Order Patellogastropoda Lindberg, 1988

#### Family Nacellidae Thiele, 1891

#### Genus *Nacella* Schumacher, 1817

**Type species:** *Patella mytilina* Helbling, 1779. Recent, southern South America.

**Discussion:** The order Patellogastropoda encompasses taxa with conical shells having numerous anatomical synapomorphies (Lindberg, 1988; Sasaki, 1998); its monophyly is strongly supported by molecular data (Harasewych & McArthur, 2000; Nakano & Ozawa, 2007; Yoon & Kim, 2007). The phylogenetic relationships of families within Patellogastropoda, however, remain uncertain (Ridgway et al., 1998; Nakano & Ozawa, 2007). Some place Nacellidae or Nacelloidea (*Nacella* + *Cellana*) in a clade with Patellidae (Powell, 1973; Sasaki, 1998), others as a sister group to Acmaeoidea (Lindberg, 1988, 1998), still others as a monophyletic clade (Koufopanou et al., 1999), possibly related to Leptidae + Pectinodontidae (Nakano &

Ozawa, 2007). Some, finally, identify nacellids as a paraphyletic group (Yoon & Kim, 2007).

*Nacella* species are characterized by shell microstructures that include an 'irregular spherulitic prismatic structure type-A' M+2 layer and a 'regularly foliated' M+1 shell layer dorsal to the myostracum, an 'irregular complex crossed foliated structure' M-1 layer ventral to the myostracum, and an absence of crossed lamellar layers [terminology of Fuchigami & Sasaki (2005); see also MacClintock (1967) and Lindberg (1988, 1998)]. Most other patellogastropods from western South America lack foliated layers, e.g., the Lottiidae Gray, 1840, including *Lottia* and *Scurria* (Lindberg, 1988, 1998; Espoz et al., 2004). The nacellid genus, *Cellana*, represented in Peru and Chile by one Pliocene species (Herm, 1969; DeVries, unpublished data), has a prismatic M+3 and foliated M+2 layer, but also has crossed lamellar structures in layers M+1 and M-1 (MacClintock, 1967; Lindberg & Hickman, 1986; Fuchigami & Sasaki, 2005). The new species of *Nacella* described herein have clearly visible prismatic structure in their M+2 layer, foliation in their M+1 layer and lack crossed lamellar layers.

#### Subgenus *Nacella* Schumacher, 1817

**Description:** Shell very thin, apex very close to anterior end (Powell, 1973).

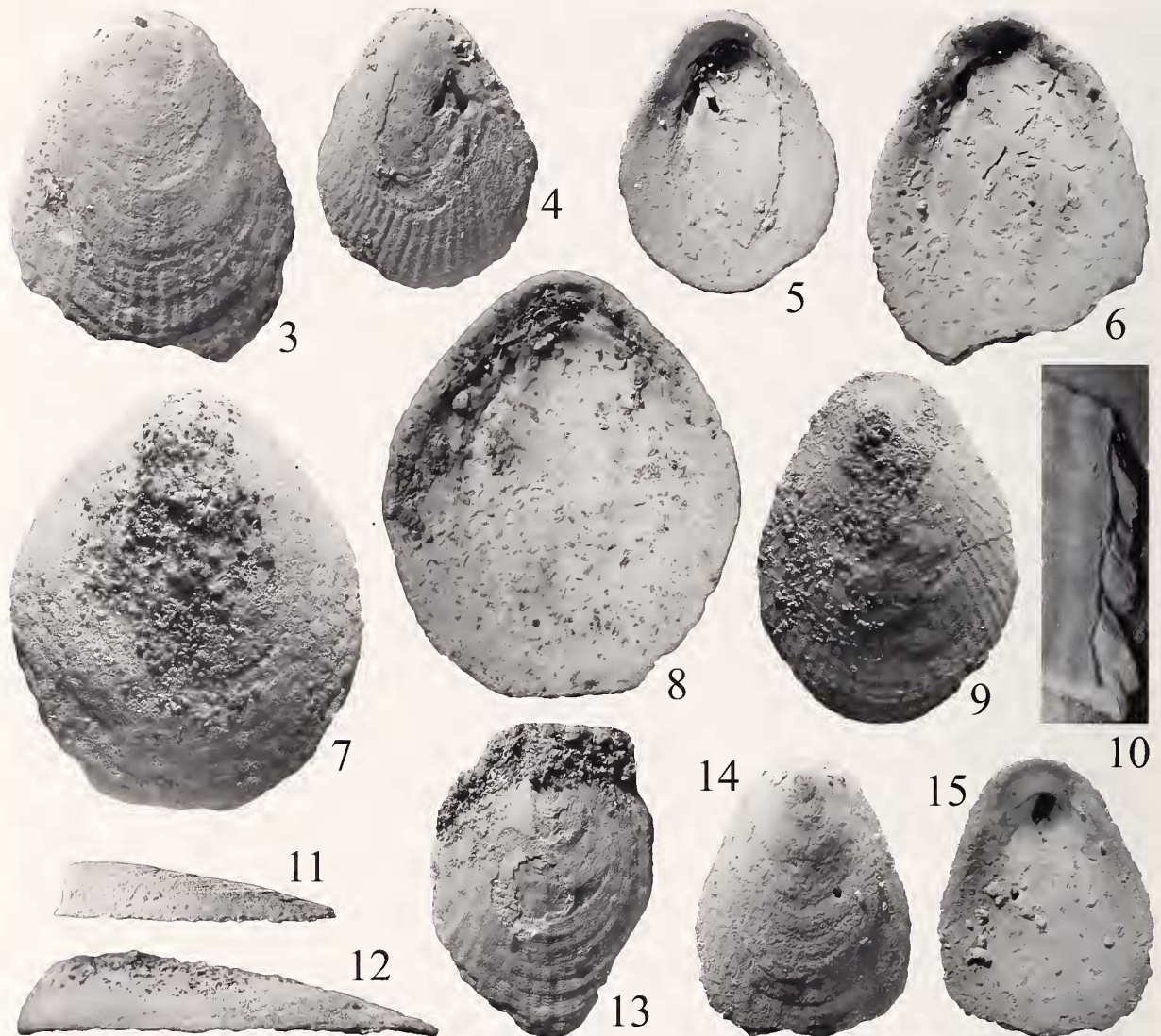
#### *Nacella (Nacella) lacrima*, sp. nov.

Figures 3–15

**Diagnosis:** Shell height extremely low. Aperture tear shaped. Radial sculpture of 60 ribs, differentiated by size posteriorly, sometimes obsolete.

**Description:** Shell conical, very thin, length under 30 mm; height extremely low (L:H ratio about 5:1 to 8:1). Aperture tear shaped: broadly elliptical posteriorly, rapidly narrowing and linear anteriorly, sharply rounded at anterior end. Shell margin planar, periphery of margin evenly curved, not crenulated. Apex orthogonal to slightly obtuse, located one-eighth or less of length from anterior end. Steep anterior slope concave, straight, or convex; posterior slope slightly convex; lateral slopes planar. Radial sculpture of up to 60 very low rounded ribs, often fewer in juveniles, obsolete in some adults; ribs not corrugated. Differentiation of primary and secondary ribs posteriorly, if present; rare secondary ribs inserted close to apex. Concentric sculpture of fine growth lines and irregular weak growth rugae. Coloring of concentric brown mottling. Interior with smooth or weakly radially striated intermediate area; central area broad and extending 80 percent of shell length.





Figures 3–15. *Nacella (Nacella) lacrima*, sp. nov. All are paratypes except holotype. DV 1279-1. Late early Pliocene.

Figure 3. MUSM INV 177. Dorsal view. Length is 17.3 mm.

Figure 4. MUSM INV 179. Dorsal view. Length is 15.4 mm.

Figure 5. MUSM INV 179. Ventral view.

Figure 6. MUSM INV 177. Ventral view. Angular pitting is from contact with sand grains.

Figure 7. MUSM INV 176. Dorsal view. Length is 25.0 mm.

Figure 8. MUSM INV 176. Ventral view.

Figure 9. UWBM 98627, holotype. Dorsal view. Length is 21.8 mm.

Figure 10. UWBM 98626. Close-up of regular foliated M + 1 layer (right) and prismatic M + 2 layer (left). Length of image is 7.4 mm.

Figure 11. UWBM 98621. Lateral view, anterior to left. Length is 9.7 mm.

Figure 12. MUSM INV 176. Lateral view, anterior to left.

Figure 13. UWBM 98620. Dorsal view. Length is 24.0 mm.

Figure 14. UWBM 98621. Dorsal view.

Figure 15. UWBM 98621. Ventral view.

**Discussion:** The extreme anterior position of the apex places this taxon in *Nacella (Nacella)*. The only other South American species in this subgenus, the Recent *N. (Nacella) mytilina*, lives throughout the Magellanic Province (Valdovinos & R uth, 2005). Its specimens are

laterally compressed, deeply arched, and have a radial sculpture of weak wrinkles. *Nacella (Nacella) kerguelensis* (E. A. Smith, 1877), a Recent species from the southern Indian Ocean (about 49°S), is nearly three times longer than *N. (Nacella) lacrima*, has a high

profile, and is not laterally compressed (Powell, 1973; Ubaldi, 1985a; note that images of *N. kerguelenensis* differ in the two references).

**Etymology:** Latin 'lacrima,' meaning 'tear,' referring to the teardrop shape of this species.

**Type Locality:** DV 1279-1, base of southeast wall of sand-and-gravel quarry along the Pan-American Highway, five km (straight distance) from village of Ocoña (Figure 1). Limpets were found in finely bedded and cross-bedded fine-grained gravel (Figures 2A–2C). 16°25'28"S, 73°09'14"W.

**Material** (all specimens from DV 1279-1, late early Pliocene; all but holotype are paratypes): MUSM INV 176, L 25.0, W 21.0, H 4.6; MUSM INV 177, L (17.3), W 13.9, H 2.2; MUSM INV 178, L 18.3, W 13.8, H 3.0; MUSM INV 179, L 15.4, W 12.0, H 2.5; UWBM 98619, L 24.8, W 21.7, H 4.3; UWBM 98620, L 24.0, W 17.1, H 3.0; UWBM 98621, L 9.7, W 7.6, H 1.9; UWBM 98622, L (7.8); UWBM 98623, holotype, L 21.8, W 16.0, H 3.9; UWBM 98624, L (7.1).

**Occurrence:** Late early Pliocene: southern Peru.

Subgenus *Patinigera* Dall, 1905

**Type species:** *Patella magellanica* Gmelin, 1791. Recent, southern South America.

**Description:** Shell more solid than *Nacella* (*Nacella*); apex closer to a central position (Powell, 1973).

*Nacella* (*Patinigera*) *oblea*, sp. nov.

Figures 16–26

**Diagnosis:** Shell very thin, height very low. Aperture nearly circular posteriorly; apex one-third of length from anterior. Radial sculpture of nearly 80 low ribs, usually with pronounced differentiation by size.

**Description:** Shell conical, very thin, length to about 40 mm; height very low (adult L:H ratio about 5:1). Aperture nearly circular posteriorly, broadly oval and slightly constricted anteriorly. Shell margin planar to slightly arched longitudinally, evenly curved with fine crenulations corresponding to primary ribs. Apex obtuse, located one-third of length from anterior end. Anterior slope usually planar, lateral and posterior slopes slightly convex. Radial sculpture of about 80 fine, low, rounded ribs near margin, including frequent distal insertions of secondary ribs; differentiation of primary and secondary ribs usually pronounced. Concentric sculpture of closely spaced, finely crenulated growth lines and irregularly spaced coarser growth rugae. Color uniformly cream. Interior faintly irides-

cent, intermediate area with fine radial striae and ridges; central area 60 to 80 percent of shell length.

**Discussion:** Specimens of *Nacella oblea* greatly resemble those of *N. clypeater* (Figures 27, 28), differing principally in being thinner, having an anterior end that is more constricted, primary and secondary ribs that are more differentiated, and a uniformly cream color. One specimen from 37 meters (Unit II) in the Huacllaco section (Figure 25) has a less constricted anterior, subdued to obsolete radial sculpture, and a purple-brown exterior like specimens of modern *N. clypeater*. Upper Pliocene Huacllaco specimens from 48 meters (Unit III) and 68 meters (Unit IV) (UWBM 98684, UWBM 98685, respectively) are thicker and the unworn specimen from Unit III has coarser radial sculpture than lower Pliocene specimens, characters that may indicate a transition had begun to typical *N. clypeater*.

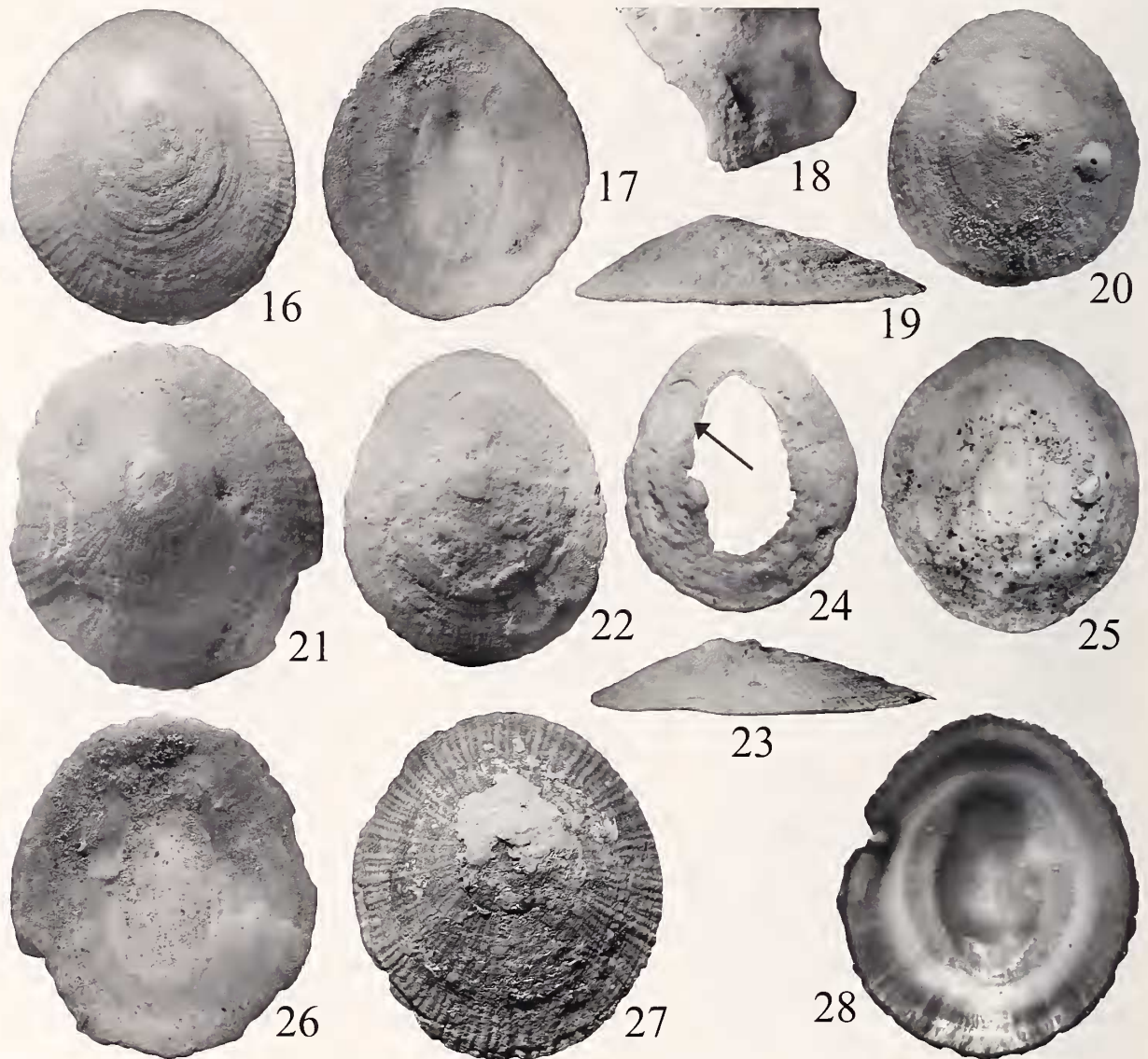
*Nacella clypeater* is the only Recent western South American *Nacella* to occur north of the Magellanic Province (Valdovinos & R uth, 2005), ranging as far north as Arica, Chile (about 18°30'S) (Ram rez-B hme, 1996) and Atico, southern Peru (about 16°12'S); almost certainly it is not found as far north as Lima or north-central Peru, as claimed by Ubaldi (1985b) (A. Indacochea, V. Mogollon, written communication, 2008). *Nacella clypeater* differs from Magellanic *Nacella* by favoring subtidal habitats, especially the 'fondos blanqueados' described in V squez & Vega (2004), expanses of subtidal substrate covered with white coralline algae (Meneses, 1993; Valdovinos, written communication, 2008). The great numbers of *N. clypeater* that congregate on the coralline blankets are usually encrusted with the algae. Oddly, though, Peruvian Pliocene specimens of *N. oblea* are entirely free of coralline encrustations, having only rare attachment scars from barnacles or *Scurria* limpets (Figure 24).

**Etymology:** Spanish 'oblea,' a Roman Catholic communion wafer, which this species resembles.

**Type Locality:** DV 1254, Huacllaco, ten km southeast of Chala along the Pan-American Highway, about 37 m in measured section (DV 1254-2; Figure 1). 15°53'25"S, 74°09'52"W.

**Material** (specimens are paratypes from DV 1254-2 and early late Pliocene unless otherwise stated): MUSM INV 180, DV 1254-bal6, L 38.2, W 31.7, H 7.2; MUSM INV 181, L 27.8, W 23.6, H 4.9; MUSM INV 182, L 29.3, W 25.4, H 5.2; MUSM INV 183, L (27.0), W 25.3, H 5.9; UWBM 98625, holotype, L 35.7, W 31.7, H 7.2; UWBM 98626, DV 1254-bal6, L 25.8, W 23.3, H 5.4; UWBM 98627, L (20.3); UWBM 98628, L 30.0, W 25.5, H (4.0); UWBM 98629, L 28.5, W 25.8, H 4.8; UWBM 98630, L 15.0, W 8.1, H 2.5; UWBM 98631,





Figures 16–26. *Nacella (Patinigera) oblea*, sp. nov. All paratypes except holotype.

Figure 16. UWBM 98629. DV 1254-2. Early late Pliocene. Dorsal view. Length is 28.5 mm.

Figure 17. MUSM INV 182. DV 1254-2. Ventral view. Length is 29.3 mm.

Figure 18. UWBM 98627. DV 1254-2. Regular foliated microstructure, first-order folia of M + 1 layer adjacent to myostracum. Width of broadened anterior end of central area (lower right) is 7.8 mm.

Figure 19. MUSM INV 180. DV 1254-bal6. Early late Pliocene. Lateral view, anterior to left. Length is 38.2 mm.

Figure 20. UWBM 98626. DV 1254-bal6. Dorsal view. Length is 25.8 mm.

Figure 21. UWBM 98625, holotype. DV 1254-2. Dorsal view. Length is 35.7 mm.

Figure 22. MUSM INV 180. Dorsal view.

Figure 23. MUSM INV 181. DV 1254-2. Lateral view, anterior to left. Length is 27.8 mm.

Figure 24. UWBM 98628. DV 1254-2. Dorsal view. Arrow points at *Scurria* scar. Length is 30.0 mm.

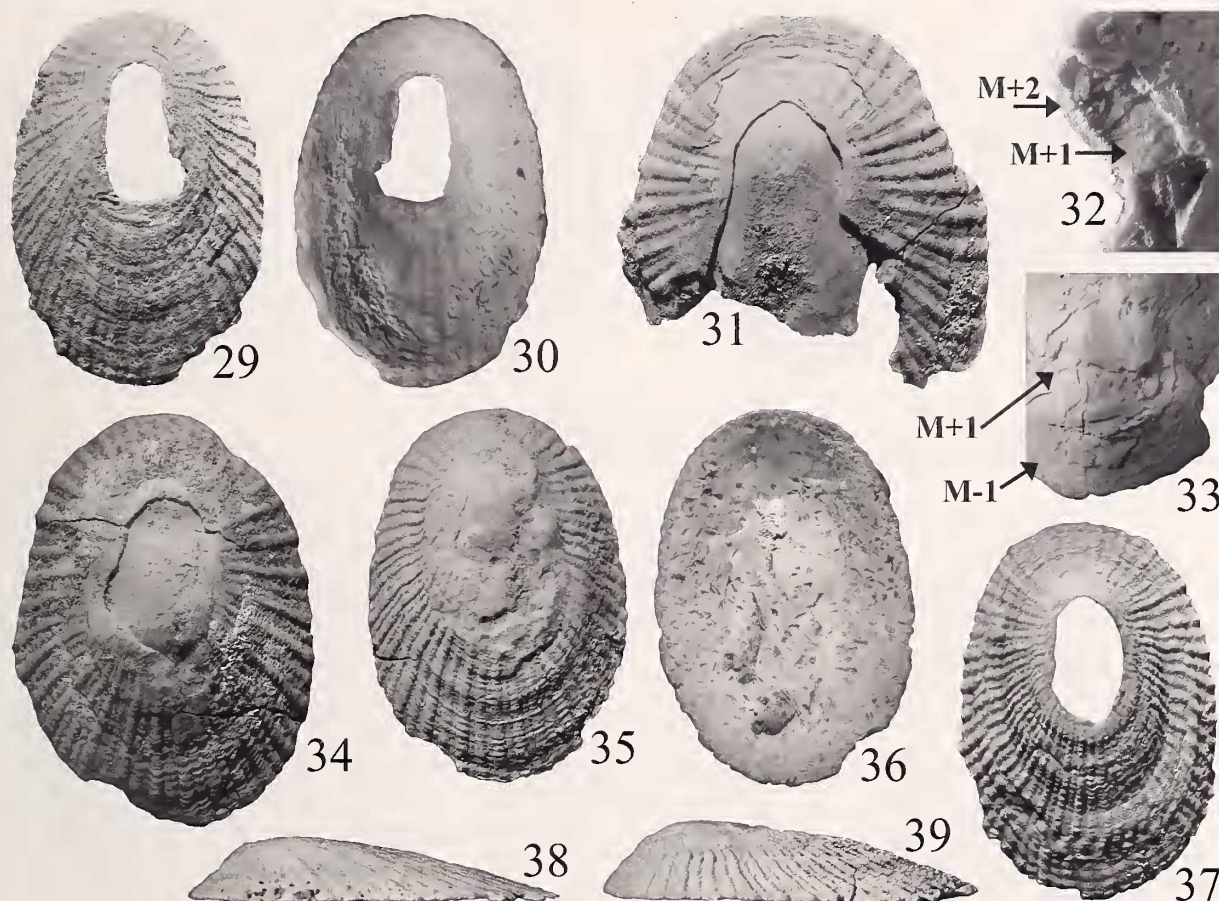
Figure 25. UWBM 98631. DV 1254-bal6. Dorsal view showing dark coloration (brown) near margin. Length is 34.6 mm.

Figure 26. UWBM 98625. Ventral view.

Figures 27, 28. *Nacella (Patinigera) clypeater* (Lesson, 1831). Pucatrihue, south-central Chile. Recent.

Figure 27. UWBM 98632. Dorsal view. Length is 38.0 mm.

Figure 28. UWBM 98633. Ventral view. Length is 43.3 mm.



Figures 29–39. *Nacella (Patinifera) intiforma*, sp. nov.

Figure 29. UWBW 98635, paratype. DV 1279-1. Late early Pliocene. Dorsal view, apex missing. Length is 33.1 mm.

Figure 30. UWBW 98635. Ventral view, central area missing.

Figure 31. UWBW 98637. DV 1267-1. Late early Pliocene. Dorsal view, posterior missing.

Figure 32. UWBW 98637. Close-up of microstructure: regular foliated M+1 layer and prismatic M+2 layer.

Figure 33. UWBW 98637. Close-up of microstructure: regular foliated M+1 layer and cross foliated M-1 layer.

Figure 34. UWBW 98636. DV 1267-1. Dorsal view. Length is 37.6 mm.

Figure 35. UWBW 98634, holotype. DV 1279-1. Dorsal view. Length is 26.6 mm.

Figure 36. UWBW 98634. Ventral view.

Figure 37. MUSM 185, paratype. DV 1279-1. Dorsal view. Length is 22.0 mm.

Figure 38. UWBW 98635. Lateral view, anterior to left.

Figure 39. UWBW 98634. Lateral view, anterior to left.

DV 1254-bal6, L 34.6, W 30.3, H 7.0; UWBW 98684, DV 1254-10, late Pliocene, L 43.2, W 41.3, H 11.1; UWBW 98685, DV 1941-1, latest Pliocene, L 43.9, W 38.4, H 11.2.

**Occurrence:** Early late Pliocene: southern Peru.

*Nacella (Patinifera) intiforma*, sp. nov.

Figures 29–39, 46

**Diagnosis:** Shell moderately thin; height very low. Aperture elliptically quadrate; aperture one-third of length from anterior. Radial sculpture of about 55 to

60 strong corrugated ribs, usually alternatingly differentiated by size anteriorly and posteriorly.

**Description:** Shell conical, moderately thin, length to about 60 mm; height very low (L:H ratio about 4:1 to 6:1). Aperture elliptically quadrate, broader posteriorly. Shell margin planar to slightly arched longitudinally, evenly curved with crenulations corresponding to ribs. Apex obtuse, located one-quarter of length from anterior end. Anterior slope steep, planar to slightly concave, posterior slope slightly convex, lateral slopes planar. Radial sculpture of about 55 to 60 ribs, differentiated by size anteriorly and posteriorly, some-



times laterally. Ribs weakly to strongly corrugated by intersections with strong concentric growth lines; corrugations somewhat irregular and not always evenly sized or spaced. Interior faintly iridescent; interior margin crenulated; central area 60 to 80 percent of shell length.

**Discussion:** Specimens of *Nacella intiforma* have a shape similar to those of *N. oconaensis*, sp. nov. (see below), but primary ribs of the latter species are fewer and coarser. Specimens of *N. intiforma* resemble small deep-water nacellids assigned by Powell (1973) to *N. (Patinigera) deaurata* form *delicatissima* (Strebel, 1907), which have equally low profiles (but see Valdovinos & R uth (2005) for statistics on higher profiles) and equally strong ribs, albeit fewer. Also similar are specimens of the strongly ribbed *N. (Patinigera) terroris* (Filhol, 1880), which are found only on sub-Antarctic Campbell Island (52°32'S, 169°09'E), near New Zealand, but these have a more centrally located apex, a much higher profile (L:H ratio about 2:1 to 3:1) and are less elongate.

Specimens similar to those of *N. intiforma* were found in early late Pliocene bioclastic deposits of the Huacllaco section (DV 1254-bal6). Ribs on the larger specimen (UWBM 98643; L 46 mm) are worn, but present in sufficient number for it to be assigned to *N. intiforma*. The anterior, posterior, and lateral slopes of the specimen are convex, but slopes closer to the apex are planar. A 30-mm long Pliocene specimen of *Nacella* was reported from south-central Chile (Le Roux et al., 2008). Photographs provided by S. Nielsen (written communication, April, 2008) reveal an apertural form, height, and nearly obsolete sculpture similar to that of the large Huacllaco example of *N. intiforma*.

**Etymology:** Quechua 'inti,' meaning sun, referring to the well formed ribs that produce a sunburst pattern on this species.

**Type Locality:** DV 1279-1, base of southeast face of sand-and-gravel quarry along the Pan-American Highway, 5 km (straight distance) from village of Ocoña (Figure 1). Limpets were found in finely bedded and cross-bedded fine-grained gravel (Figures 2A–2C). 16°25'28"S, 73°09'14"W.

**Material** (all specimens late early Pliocene): MUSM INV 184, DV 1279-1, paratype, L 20.9, W 13.8, H 3.3; MUSM INV 185, DV 1279-1, paratype, L 22.0, W 14.8, H (3.7); MUSM INV 186, DV 1267-1, L (25.9); UWBM 98634, DV 1279-1, holotype, L 26.6, W 18.6, H 4.8; UWBM 98635, DV 1279-1, paratype, L 33.1, W 22.6, H (5.5); UWBM 98636, DV 1267-1, L 37.6, W 27.7, H 9.2; UWBM 98637, DV 1267-1, L (35.2), W 35.8, H (9.0); UWBM 98638, DV 1045-1, L 60.4, W 46.0, H 8.1; UWBM 98643, DV 1254-bal6, L (46.3), W

38.7, H 10.4; UWBM 98644, DV 1254-bal6, L 23.1, W (17.0), H 4.0.

**Occurrence:** Late early Pliocene to early late Pliocene: southern Peru, south-central Chile.

*Nacella (Patinigera) oconaensis*, sp. nov.

Figures 40–45, 47, 48

**Diagnosis:** Shell thick, height low. Aperture elliptical to oval; apex one-third of length from anterior. Radial sculpture of about 30 to 40 strong but weakly corrugated ribs, usually differentiated by size laterally and posteriorly.

**Description:** Shell conical, moderately thick, length to about 50 mm; height low (H:L ratio 4:1 to 5:1). Aperture elliptical to oval, broader posteriorly. Shell margin evenly curved, sometimes deformed; longitudinally planar to arched; with crenulations corresponding to ribs. Apex obtuse, located one-quarter to one-third of length from anterior end. Anterior slope steepest, all adult slopes planar to slightly convex; break in slope separates more elevated juvenile stage. Radial sculpture of about 30 to 40 primary ribs, with insertion of secondary ribs posteriorly and laterally, generally not anteriorly. Ribs weakly corrugated at intersections with fine concentric growth line crenulations and coarser rugae. Interior margin crenulated; intermediate area smooth; central area about 60 to 80 percent of shell length.

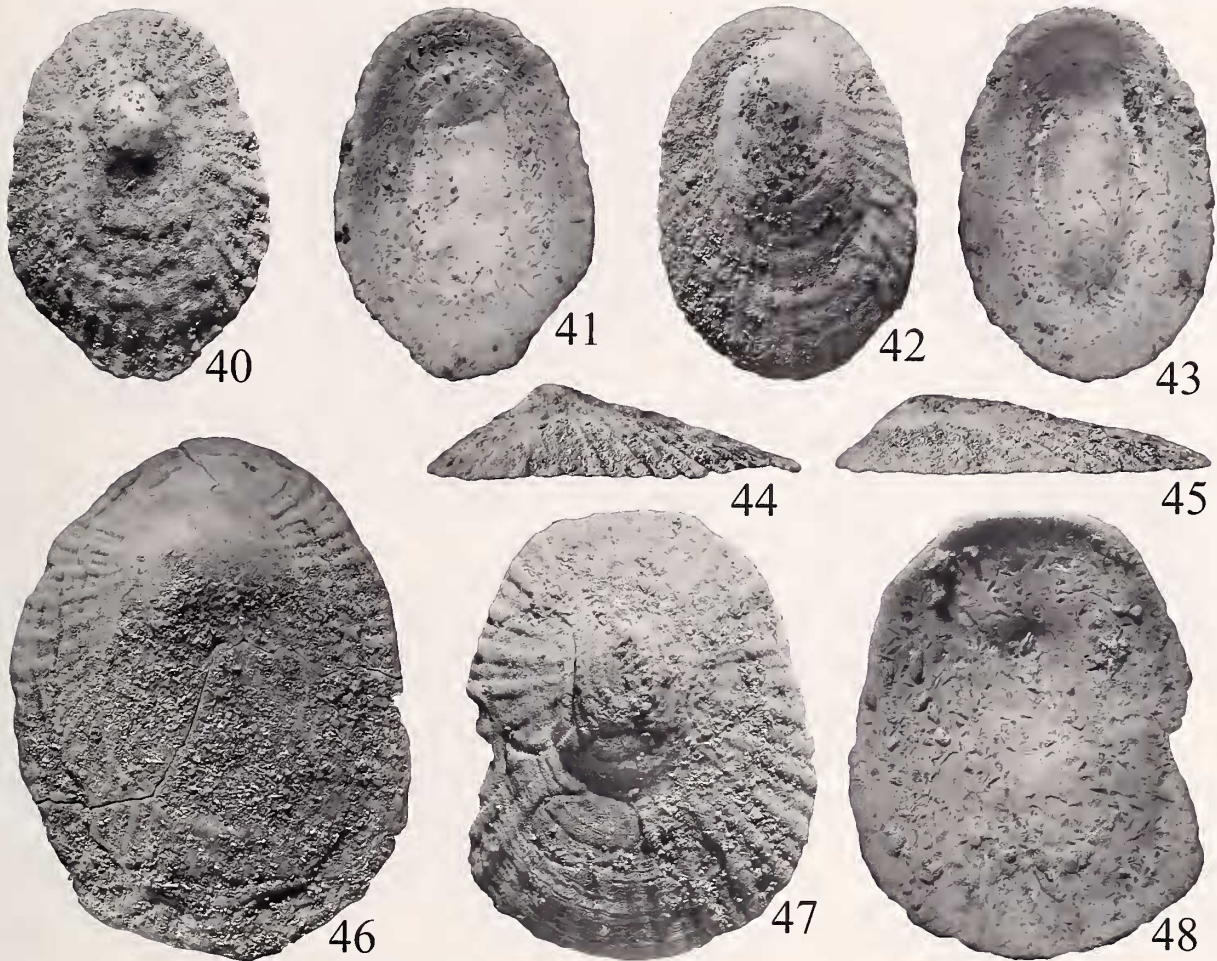
**Discussion:** Specimens of *Nacella (Patinigera) oconaensis* at the type locality (DV 1279-1) resemble those of *N. intiforma*, with which they occur, but they are thicker and have fewer and coarser ribs. Both taxa may be ecophenotypic variants of the same species.

The radial sculpture and rib number of *Nacella oconaensis* match those of extant *N. (Patinigera) macquariensis* Finlay, 1927, from Macquarie Island (54°30'S, 159°E) and Heard Island (53°S, 74°E) (Powell, 1973), but the latter species has a much higher profile (L:H ratio about 2:1).

**Etymology:** Named for Ocoña, a nearby village.

**Type Locality:** DV 1279-1, base of southeast face of sand-and-gravel quarry along the Pan-American Highway, 5 km (straight distance) from village of Ocoña (Figure 1). Limpets were found in finely bedded and cross-bedded fine-grained gravel. 16°25'28"S, 73°09'14"W.

**Material** (all localities except DV 1254-bal6 are late early Pliocene): MUSM INV 187, DV 1279-1, paratype, L 30.7, W 21.9, H 6.8; MUSM INV 188, DV 1254-bal6, early late Pliocene, L 19.9, W 12.5, H 3.7; UWBM 98639, DV 1279-1, holotype, L 29.7, W 20.6, H 5.5; UWBM 98640, DV 1279-1, paratype, L 17.9, W



Figures 40–45, 47, 48. *Nacella (Patinifera) oconaensis*, sp. nov.

Figure 40. MUSM INV 187, paratype. DV 1279-1. Late early Pliocene. Dorsal view. Length is 30.7 mm.

Figure 41. MUSM INV 187. Ventral view.

Figure 42. UWBM 98639, holotype. DV 1279-1. Dorsal view. Length is 29.7 mm.

Figure 43. UWBM 98639. Ventral view.

Figure 44. MUSM INV 187. Lateral view, anterior to left.

Figure 45. UWBM 98639. Lateral view, anterior to left.

Figure 46. *Nacella (Patinifera) intiforma*, sp. nov. UWBM 98638. DV 1045-1, late early Pliocene. Dorsal view showing growth line scars and deformed aperture. Length is 60.4 mm.

Figure 47. UWBM 98641, paratype. DV 1279-1. Dorsal view, showing deformed aperture and six scars from epibiotic limpet, *Scurria*. Length is 28.6 mm.

Figure 48. UWBM 98641. Ventral view.

13.1, H 3.9; UWBM 98641, DV 1279-1, paratype, L 28.6, W 22.5, H 6.5.

**Occurrence:** Late early Pliocene to early late Pliocene; southern Peru.

*Nacella (Patinifera) chalaensis*, sp. nov.

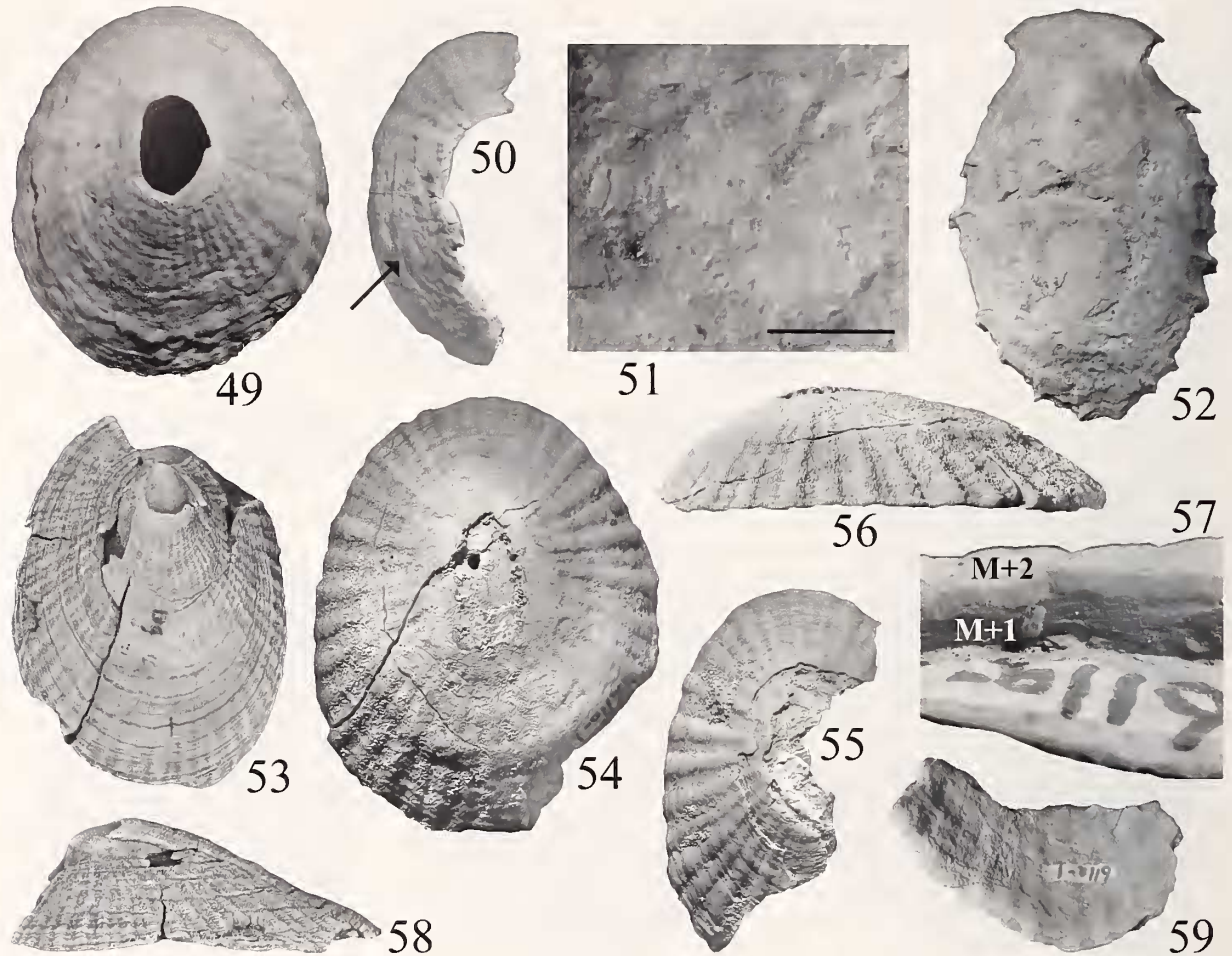
Figures 49, 50

**Diagnosis:** Shell broadly oval. Apex located two-fifths of length from anterior end. Radial sculpture of about

45 weakly nodular ribs; secondary ribs absent or barely differentiated by size.

**Description:** Shell conical, estimated length to 50 mm, height low (L:H ratio about 4:1). Aperture broadly oval, slightly constricted anteriorly. Shell margin planar to arched longitudinally, evenly curved with weak crenulations corresponding to coarsest ribs. Apex obtuse, located two-fifths of length from anterior end. Anterior and posterior slopes planar, lateral slopes slightly convex. Radial sculpture of about 45 low





Figures 49, 50. *Nacella (Patinigera) chalaensis*, sp. nov. Late early Pliocene.

Figure 49. UWBM 98686, holotype. Dorsal view. Length is 40.0 mm.

Figure 50. UWBM 98642, paratype. Dorsal view, fragment. Arrow points at *Scurria* scar. Length is 46.4 mm.

Figures 51, 52. *Nacella (Patinigera)* sp. indet. UWBM 98687. Early late Pliocene.

Figure 51. Foliated M-1 layer, ventral surface of central area. Scale bar is 1 mm.

Figure 52. Dorsal view, central area. Length is 66.2 mm.

Figures 53, 58. *Nacella (Patinigera) nielsenii*, sp. nov. WM 10612, holotype. Chiloé, southern Chile. Late early Miocene.

Figure 53. Dorsal view. Length is about 35 mm.

Figure 58. Lateral view, anterior to left.

Figures 54-57, 59. *Nacella (Patinigera) reicheae*, sp. nov.

Figure 54. UWBM 98645, holotype. DV 611a-1. Late Oligocene. Dorsal view. Length is 54.3 mm.

Figure 55. MUSM 189, paratype. DV 638-1. Late Oligocene. Dorsal view, right side and posterior missing. Length is 48.5 mm.

Figure 56. UWBM 98645. Lateral view, anterior to left.

Figure 57. UWBM 98645. Close-up of prismatic M+2 outermost layer and regular foliated M+1 layer.

Figure 59. UWBM 98647. DV 611a-1. Ventral view showing weak internal ribbing. Width is 32.0 mm.

rounded primary ribs, all variably nodose, fading towards margin. Secondary ribs absent or negligibly differentiated from primary ribs. Concentric sculpture of regularly spaced growth lines accentuating nodes and irregularly spaced growth breaks. Color cream proximal to apex, pale brown distally. Interior with weakly developed radial ribs; central area missing.

**Discussion:** Specimens of *Nacella chalaensis* are nearly

as broadly oval as those of the late Pliocene *N. oblea* and modern *N. clypeater*, but the ribs are fewer, broader, and weakly nodose; they are also broader anteriorly than all but deformed specimens of *N. intiforma* and *N. oconaensis*; the former has many more ribs, whereas the latter has a number equal to that of *N. chalaensis*. Additional material may reveal that morphological continua exist amongst specimens of *N. chalaensis*, *N. oconaensis* and *N. intiforma*.

Specimens of *Nacella chalaensis* from Unit I are the oldest from Huacllaco. They are assigned a late early Pliocene age based on associated mollusks (*Acanthina triangularis* DeVries, 2003; *Concholepas kieneri* Hupé, 1854; *Xanthochorus eripeponis* DeVries, 2005) (DeVries, 1995, 2003, 2005).

**Etymology:** Named for the nearby town of Chala.

**Type Locality:** DV 1628, Huacllaco, ten km southeast of Chala along the Pan-American Highway, less than 5 meters above the transition from orange sandstones of the Pisco Formation to balanid coquina of the La Planchada Formation (DV 1628-1; Figure 1). 15°53'25"S, 74°09'52"W.

**Material:** UWBM 98686, DV 1628-1, holotype, late early Pliocene, L 40.0, W 33.8, H 8.4; UWBM 98642, DV 1628-1, paratype, L (46.4).

**Occurrence:** Late early Pliocene: southern Peru.

*Nacella (Patinigera)*, sp. indet.

Figures 51, 52

**Discussion:** Two incomplete specimens of *Nacella*, one with a central area exceeding 66 mm in length, were discovered in 2008 by Liz Nesbitt (Burke Museum of Natural History and Culture, University of Washington, USA) in talus from basal beds of Unit III at Huacllaco. The estimated length of the largest specimen is 80–90 mm, larger than any other fossil or modern *Nacella*, excepting *N. (Nacella) kerguelensis*. The foliated M–1 layer (Figure 51) distinguishes the Huacllaco specimens from Peruvian and Chilean Pliocene specimens of *Cellana fuenzalidai* (Herm, 1969). The apex, located about one-quarter to one-third of the length from the anterior, indicates an assignment to *N. (Patinigera)* rather than *N. (Nacella)*.

**Material (all specimens from Huacllaco (DV 1929-1, early late Pliocene):** UWBM 98687, L (66.2), W (42.5); UWBM 98688, L (44.9), W (29.8); UWBM 98689, L (66.3).

**Occurrence:** Early late Pliocene: southern Peru.

*Nacella (Patinigera) nielsenii*, sp. nov.

Figures 53, 58

*Patinigera* aff. *terroris* (Filhol). Fleming, in Watters & Fleming, 1972, p. 390, pl. 28, fig. 6a.

**Diagnosis:** Shell with high profile. Apex recurved, about one-sixth of length from anterior end. Radial sculpture of about 55 strong corrugated ribs.

**Description:** Shell conical, moderately thick, length

about 40 mm; moderately high profile (L:H ratio 3:1). Aperture ovate, broader posteriorly. Shell margin evenly curved, with crenulations corresponding to ribs. Apex recurved, located one-sixth length from anterior end. Anterior slope steepest, planar below recurved apex; posterior slope planar. Radial sculpture of 56 strong, broadly rounded, corrugated ribs, with secondary ribs sometimes formed laterally from interspaces. Corrugations at intersections with strong concentric growth lines; concentric growth rugae also present. Interior unknown.

**Discussion:** A single nacellid specimen was collected on the west coast of Chiloé, Chile (42°S) by Watters & Fleming (1972). Fleming referred this limpet and other mollusks from Chiloé to the Pliocene, but the co-occurrence of *Acanthina katzi* (Fleming, 1972) and *Testallium cepa* (Sowerby, 1846) [misidentified as '*Chorus* aff. *blainvillei* (d'Orbigny)' by Fleming; see DeVries (1997) and Vermeij & DeVries (1997)] indicates an age between latest Oligocene and early middle Miocene (DeVries, 2003; DeVries & Frassinetti, 2003). The presence of the venerid bivalve *Amiantis* Carpenter, 1884, is not evidence for a Pliocene age, as was inferred by Fleming, because the genus, in addition to being represented by *A. domeykoana* (Philippi, 1887) in Pliocene beds from Chile (Philippi, 1887; Herm, 1969) and southern Peru (Muizon & DeVries, 1985), also occurs in lower Miocene to upper Miocene deposits of southern Peru (DeVries, unpublished data). Recent <sup>87</sup>Sr/<sup>86</sup>Sr isotopic analyses of shell material from *A. katzi* and *Lanprodomina dimidiata* (Sowerby, 1846) from western Chiloé have yielded ages of about 16 to 19 Ma (Nielsen & Golodny, 2006), consistent with molluscan biostratigraphic data (DeVries & Frassinetti, 2003). Hence, the single specimen of *N. nielsenii* is assigned a late early Miocene age.

The anterior position of the apex, fine corrugations and faded ribs across the posterior slope of *Nacella (Patinigera) nielsenii* recall specimens of *N. (Nacella) lacrima*, although the latter is extremely flattened and has an apex even farther anteriorward. The Chiloé specimen also resembles *N. (Nacella) kerguelensis*, which has an equally high profile but an apex also closer to the anterior end. Given its early Miocene age, its radial sculpture like that of *N. lacrima* and *N. kerguelensis*, and its apical position intermediate between species of *N. (Nacella)* and *N. (Patinigera)*, *N. nielsenii* may be the known *Nacella* closest to the evolutionary divergence of the two subgenera. Compared to its consubgenera, the modern *N. (Nacella) mytilina* appears to be a highly derived species with a loss of typical nacellid ribs and an acquired lateral compression unique for all *Nacella*.

**Etymology:** Named in recognition of Dr. Sven Nielsen



and his contributions to our knowledge of Cenozoic mollusks in Chile.

**Type Locality:** Locality E: "isolated stack, southeast side of Punta Ahuenco" (Fleming, in Watters & Fleming, 1972, p. 380). 42°06'29"S, 74°03'19"W (Google Earth).

**Material:** WM 10612, holotype, L 35, W 26, H 12.

**Occurrence:** Late early Miocene: Chiloé, southern Chile.

*Nacella (Patinigera) reicheae*, sp. nov.

Figures 54–57, 59

**Diagnosis:** Shell with low profile, apex about one-third of length from anterior end. Radial sculpture of about 35 strong and broadly rounded corrugated ribs.

**Description:** Shell conical, moderately thick, estimated length about 80 mm; height low (H:L ratio about 5:1). Aperture elliptical. Shell margin evenly curved, elevated postero-laterally, with crenulations corresponding to ribs. Apex obtuse, located one-third of length from anterior end. All slopes planar to convex. Radial sculpture of about 35 strong, broad rounded ribs, with interspaces only somewhat less wide, in some cases raised into a low secondary rib. Ribs finely corrugated by intersecting growth lines. Interior margin sometimes flattened, crenulated; intermediate area scored by broad grooves corresponding to exterior ribs; central area covered. Layers include prismatic M+2, prominent first-order foliation in M+1, and less well defined foliation in M–1.

**Discussion:** The outermost layer of *Nacella reicheae* has curved first-order crystals without sharply defined edges, consistent with the 'irregularly spherulitic prismatic structure type-A' of the M+2 layer in *Nacella* (Fuchigama & Sasaki, 2005). The underlying broad low-dipping folia match those in the 'regularly foliated' M+1 layer of *Nacella* (Figure 57). Short folia in packets at differing angles and oriented more steeply than those in the M+1 layer resemble 'crossed foliated' layers of Fuchigama & Sasaki (2005). No vertical crossed lamellar structures were observed, thereby precluding an assignment of this taxon to *Cellana* or any genus of Lottiidae (MacClintock, 1967; Lindberg, 1988, 1998; Fuchigama & Sasaki, 2005).

All specimens of *Nacella reicheae* were found near Cerro Poroma in several meters of bioclastic sandstone and gravel blanketing a fissure-riddled peneplain carved from upper Cretaceous plutonic rocks. The seaward-sloping erosional surface is a product of the late Eocene Incaic Orogeny (Noble et al., 1979b). Overlying continental volcanoclastic sediments of the

Nazca Group contain intercalated ash beds dated at 18 to 23 Ma (Noble et al., 1979a).

The presence of *Turritella woodsi* Lisson, 1925, led Rivera (1957) to assign an Eocene age to the Poroma molluscan fauna, but the range of *T. woodsi* is now properly understood to be latest Eocene (Otuma Formation) to early Miocene (lower Chilcatay Formation) (DeVries, 1998; DeVries et al., 2006). The additional occurrence in the Poroma beds of *Testallium cepa*, misidentified as *Peruficus* Olsson, 1932, in more southerly 25-Ma deposits (Noble et al., 1985; DeVries, 2001a) that were also mis-assigned to the Eocene by Petersen (1954) and Pecho (1983), indicates a latest Oligocene to early middle Miocene age for the *Nacella*-bearing beds (Vermeij & DeVries, 1997; DeVries & Frassinetti, 2003). A latest Oligocene age for the Poroma specimens of *Nacella reicheae* is proposed, it being consistent with molluscan ranges, <sup>40</sup>K-<sup>40</sup>Ar dates, and the presumed synchronicity of a latest Oligocene transgressive event across the coastal margin of southern Peru (DeVries, 1998, 2001a).

The two largest specimens attributed to *Nacella reicheae* (UWBM 98646, UWBM 98650) are partially and poorly preserved. That they are patellogastropods and nacellids is without doubt, since one exhibits a continuous shell layer across the apex and both have a well developed foliated M+1 layer and prismatic M+2 layer. The high profile of one specimen and coarse radial sculpture of both specimens, however, may be evidence that a second species of Oligocene *Nacella* occupied the Poroma peneplain, thereby implying that the southern Peruvian coast may have been populated by a diverse but poorly preserved *Nacella* fauna since at least 25 Ma.

**Etymology:** Named in honor of the late Dra. Maria Reiche, who dedicated 50 yr to the study and preservation of the nearby Nazca lines.

**Type Locality:** DV 611a-1, midpoint of the northwestern flank of Cerro Poroma (Figure 1), at the contact between crystalline basement rock and an overlying sedimentary sequence (Figure 2F). 14°59'58"S, 74°59'08"W (Google Earth).

**Material (all specimens late Oligocene; all specimens paratypes except holotype):** MUSM INV 189, DV 638-1, L (48.5), H (10.7); UWBM 98645, DV 611a-1, holotype, L 54.3, W 42.4, H 11.9; UWBM 98646, DV 611a-1, L (62.4); UWBM 98647, DV 611a-1, W (37.2); UWBM 98648, DV 611a-1, W (32.0); UWBM 98649, DV 638-1, W (36.8); UWBM 98650, DV 471-1, L (66.0), W (55.2), H (22.5).

**Occurrence:** Late Oligocene: southern Peru.

## DISCUSSION

Biogeographic constraints on Pliocene *Nacella*

Most modern limpets in temperate waters between Chiloé (42°S) and Trujillo (8°S), i.e., the Peruvian Faunal Province, are species of *Fissurella* (Vetigastropoda: Fissurellidae) or *Scurria* (Patellogastropoda: Lottiidae) (McLean, 1984; Alamo & Valdivieso, 1997; Espoz et al., 2004). Modern mean annual SSTs in this region range between 14°C and 20°C. Most modern limpets from Pacific shores of the Magellanic Faunal Province (Chiloé to Cape Horn) belong to the genera *Fissurella*, *Scurria*, and *Nacella*. These limpets experience mean annual SSTs between 7°C and 14°C. *Nacella* from Antarctica, the Scotia Arc, and Heard, Kerguelen, Macquarie, and Campbell Islands endure mean annual SSTs under 8°C. Such data would imply that *Nacella* is a cold-water genus (Powell, 1973; Lindberg, 1988; Nakano and Ozawa, 2007), excepting only the Chilean *N. (Patinigera) clypeater*, which ranges north (Ramírez-Böhme, 1996; Valdovinos & Rüth, 2005; A. Indacochea and V. Mogollon, written communications, 2008) into waters with a mean annual SST of up to 19°C.

Pliocene limpets of southern Peru belong to *Fissurella* (DeVries, 2008), *Nacella*, and *Scurria* (recognized from epibiotic scars on *Fissurella* and *Nacella*; see Figures 24, 47 and 50). The presence of at least five *Nacella* species at 16°S, representing both *N. (Nacella)* and *N. (Patinigera)*, challenges the idea that *Nacella* is an obligate cold-water taxon. Typical modern seasonal SSTs along the southern Peruvian margin range between 14°C (winter) and 22°C (summer) (Instituto del Mar del Perú; [http://200.60.133.147/luprsig/sst\\_prov.html](http://200.60.133.147/luprsig/sst_prov.html); April, 2008). Pliocene SSTs are likely to have been warmer, inasmuch as the early Pliocene and even late Pliocene global ocean and atmosphere were warmer than at present (Zachos et al., 1996; Dowsett et al., 1999; Ravelo et al., 2004). The presence of warm-water molluscan taxa in southern Peru and Chile during the early Pliocene [e.g., *Dosinia ponderosa* (Schumacher, 1817), *Chionopsis* sp., *Protothaca asperirina* (Sowerby, 1835), *Northia* sp., *Terebra* sp., and *Cancellaria* spp. (Herm, 1969; Muizon & DeVries, 1985; DeVries, 2001b, unpublished data) and their absence since the late Pliocene further indicates warmer SSTs prevailed while Pliocene *Nacella* occupied southern Peruvian shores.

With Pliocene *Nacella* so successful in warm waters at tropical latitudes, a reason unrelated to SSTs is needed to explain their presence in southern Peru, e.g., a paleogeographic reason. Modern *Nacella* are most diverse in Magellanic fjords, the consequence, Valdovinos & Rüth (2005) speculated, of habitat fragmentation during Pleistocene cycles of eustatic sea-level change. Fjords would also afford *Nacella* protection

from the most energetic waves of the Pacific Ocean. Such protection does influence the distribution of modern *Nacella*. Chilean species with high shells and strong pedal muscles live in exposed intertidal settings, while those with low thin shells and small pedal muscles inhabit quieter subtidal environments (Valdovinos & Rüth, 2005; but note the low profile of *N. clypeater* specimens from exposed beaches at Pucatrihue, south-central Chile; UWBM 98632, 98633). Similar distributional patterns have been observed for sub-Antarctic populations of *N. concinna* (Beaumont & Wei, 1991; Nolan, 1991) and *N. macquariensis* (Simpson, 1985) and Argentinean populations of *N. deaurata* (Morriconi & Calvo, 1993).

Protected paleo-embayments with sand and cobble substrates could have provided Pliocene Peruvian *Nacella* with quiet waters near Acari, Aguada de Lomas, and Nazca (Muizon & DeVries, 1985; DeVries, 1988). Of these embayments, however, only the largest, near Nazca, has yielded a limpet: a massive *Lithoplaga*-bored *Cellana fuenzalidai* from the lee side of a Pliocene peninsula. The five Peruvian *Nacella*, in contrast, whose low profile might otherwise indicate life in a protected setting, lived along an exposed cliff-lined coast like that which has prevailed throughout the Quaternary. About three-quarters of the specimens from these five Pliocene species show break-and-repair scars along their present or former margins, a proportion comparable to those for exposed populations of *N. concinna* in the South Shetland Islands and *N. delesserti* (Philippi, 1849) on Marion Island and much less than that for a quiet-water population of *N. deaurata* from the Falkland Islands (Cadée, 1999). The Pliocene taxa of southern Peru, it seems, did live a life exposed to high-energy waves, a situation that persists today, although only one species of *Nacella* now lives there.

A change in the ecological landscape might explain the late Pliocene demise of Peruvian *Nacella*. Littoral molluscan faunas suffered a mass extinction during the late Pliocene (DeVries, 2001b), a time when patterns of competition for space and food would have been radically altered, as well as the interactions between a changing cast of predators and prey. Barnacles, for example, presently play a complex role in the settlement and success of modern keyhole limpets (Lopez et al., 1999). The dominance of barnacle species in southern Peru shifted considerably during the late Pliocene (DeVries, unpublished data), with possible impacts on the viability of *Nacella* populations. Coralline algae are an important food for some *Nacella* (Vásquez & Vega, 2004; Valdovinos, written communication, 2008), as are the fronds and spores of kelp (Blankley & Branch, 1985). Changes in their distribution could also explain the late Pliocene disappearance of Peruvian *Nacella*. In Antarctica, kelp gulls (*Larus*) prey heavily upon



intertidal *Nacella* (Branch, 1985; Cadée, 1999), as do fish (Blankley, 1982). Increased predation of intertidal organisms could have affected the survival of Peruvian *Nacella*. All of these hypotheses are plausible, but to date, none has been investigated.

### Origin of *Nacella*

Molecular and morphological data show *Nacella* and *Cellana* share a common ancestor (e.g., Lindberg, 1988; Nakano & Ozawa, 2007). A southern origin for *Nacella* + *Cellana* (= Nacellidae) has been proposed (Koufopanou et al., 1999; Nakano & Ozawa, 2007) based on accounts of Eocene *Cellana* from Seymour Island, Antarctic Peninsula (Stillwell & Zinsmeister, 1992), New Zealand (Beu et al., 1990) and unconfirmed *Cellana* from Cretaceous beds of Australia (Powell, 1973). Nevertheless, the oldest fossils of *Cellana* verified by shell microstructure lived during the late Eocene in the northeastern Pacific Ocean (Lindberg & Hickman, 1986) and the oldest fossils of *Nacella*, likewise verified by shell microstructure, lived during the late Oligocene at tropical latitudes in Peru (this report). A Tethyan origin for Nacellidae is therefore a stronger possibility than when the idea was rejected by Koufopanou et al. (1999). Furthermore, the Pliocene history of *Nacella* in western South America is a cautionary tale for those who would invoke the modern diversity of austral *Nacella* as proof of a southern high-latitude origin. At least five Pliocene species of *Nacella* lived in southern Peru when its shores were bathed by water over 20°C. Their extinction by the end of the Pliocene produced a modern Weddellian distribution (*sensu* Zinsmeister, 1982) for the genus, but one of only relatively recent vintage.

Because of the Eocene age for the Oregonian *Cellana*, the timing for the evolutionary separation of *Nacella* and *Cellana* was set prior to 38 Ma by Koufopanou et al. (1999) and Goldstien et al. (2005). If, however, the shell microstructure of *Cellana* is plesiomorphic and if the complete loss of crossed lamellar microstructure in *Nacella* is a synapomorphy of *Nacella* alone, two possibilities raised by Koufopanou et al. (1999), then a clade of modern *Nacella* taxa could be a sister group to all modern *Cellana* but not to the group of Eocene + modern *Cellana*. *Cellana*, in other words, could be a paraphyletic group encompassing Eocene *Cellana*, modern *Cellana*, and all *Nacella*. If true, *Nacella* could have evolved more recently than 38 Ma. The discovery of a 25-Ma *Nacella* in southern Peru, however, limits how recently the *Cellana*/*Nacella* split could have occurred. With late Oligocene *Nacella* in Peru, early Miocene *Nacella* in Chile, and with South America a center of Pliocene and Quaternary *Nacella* diversity, it is possible that tropical

western South America was the region where the first *Nacella* appeared.

### CONCLUSIONS

At least six new species of low-profile *Nacella* limpets from southern Peru, at least five Pliocene and one late Oligocene, and one *Nacella* from southern Chile, reassigned to the early Miocene, expand the record of this famously cold-water austral genus into tropical warmer-water latitudes of the southeastern Pacific Ocean. These taxa were collected from beds whose texture and sedimentary structures indicate high-energy littoral settings, although the low apex of most species suggests some moderation of that energy. The origin of *Nacella* remains a mystery, although these new accounts of *Nacella* establish that its present sub-Antarctic diversity does not exclude the possibility of an origin at lower latitudes, a possibility further strengthened by the presence of its nacellid sister group, *Cellana*, in the northern hemisphere during the late Eocene.

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### REFERENCES

- ADAMS, H. 1869. Descriptions of a new genus and fourteen new species of marine shells. *Proceedings of the Zoological Society of London* (1869):272–275.
- AGUIRRE, M. L., S. RICHIANO & Y. N. SIRCH. 2006. Palaeoenvironments and palaeoclimates of the Quaternary molluscan faunas from the coastal area of Bahía Vera-Camarones (Chubut, Patagonia). *Palaeogeography Palaeoclimatology Palaeoecology* 229(4):251–286.
- AGUIRRE, M. L., Y. N. SIRCH & S. RICHIANO. 2005. Late Quaternary molluscan assemblages from the coastal area of Bahía Bustamante (Patagonia, Argentina): Paleocology and paleoenvironments. *Journal of South American Earth Sciences* 20:13–32.
- ALAMO, V. & V. VALDIVIESO. 1997. Lista sistemática de moluscos marinos del Perú. Instituto del Mar del Perú: Callao, Peru. 183 pp.
- BEAUDET, G., D. HERM, R. LAHARIE & R. PASKOFF. 1976. Sur l'existence du Pliocène marin le long de la côte du Sud

- du Pérou. Société Géologique de France, Comptes Rendus Sommaires des Séances 1:12–13.
- BEAUMONT, A. R. & J. H. C. WEI. 1991. Morphological and genetic variation in the Antarctic limpet *Nacella concinna* (Strebel, 1908). *Journal of Molluscan Studies* 57(4):443–450.
- BEU, A. G. & P. A. MAXWELL. 1990. Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin* 58:518.
- BLANKLEY, W. O. 1982. Feeding ecology of three inshore fish species at Marion Island (Southern Ocean). *South African Journal of Zoology* 17(4):164–170.
- BLANKLEY, W. O. & G. M. BRANCH. 1985. Ecology of the limpet *Nacella delesserti* (Philippi) at Marion Island in the sub-Antarctic Southern Ocean. *Journal of Experimental Marine Biology and Ecology* 92(2–3):259–281.
- BRANCH, G. M. 1985. The impact of predation by kelp gulls *Larus dominicanus* on the sub-Antarctic limpet *Nacella delesserti*. *Polar Biology* 4(3):171–177.
- BRUNET, R. F. J. 1997. New species of Mollusca from the Entrerriense Formation (Upper Miocene) of Chubut Province, Argentina and species not previously reported from this formation. Part II - Gastropoda. *Tulane Studies in Geology and Paleontology* 30(2):61–98.
- CADÉE, G. C. 1999. Shell damage and shell repair in the Antarctic limpet *Nacella concinna* from King George Island. *Journal of Sea Research* 41:149–161.
- CANTALAMESSA, G. & C. DI CELMA. 2005. Sedimentary features of tsunami backwash deposits in a shallow marine Miocene setting, Mejillones Peninsula, northern Chile. *Sedimentary Geology* 178:259–273.
- DALL, W. H. 1905. Notes on some preoccupied names of mollusks. *The Nautilus* 118(10):113.
- DEVRIES, T. J. 1988. Paleoenvironments of the Pisco Basin. Pp. 141–150 in R. B. Dunbar & P. A. Baker (eds.), *Cenozoic geology of the Pisco Basin*. Guidebook to Regional IGCP 156 Field Workshop, genesis of Cenozoic phosphorites and associated organic-rich sediments: Peruvian continental margin. Lima, Peru, May 16–25, 1988.
- DEVRIES, T. J. 1995. *Concholepas* Lamarck, 1801 (Neogastropoda: Muricoidea): A Neogene genus native to South America. *The Veliger* 38(4):284–297.
- DEVRIES, T. J. 1997. A review of the genus *Chorus* Gray, 1847 (Gastropoda: Muricidae) from western South America. *Tulane Studies in Geology and Paleontology* 30(3):125–147.
- DEVRIES, T. J. 1998. Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). *Journal of South American Earth Sciences* 11(3):217–231.
- DEVRIES, T. J. 2001a. Molluscan evidence for an Oligocene-Miocene age of 'Paracas' beds in southern Peru. *Boletín de la Sociedad Geológica del Perú* 92:57–65.
- DEVRIES, T. J. 2001b. Contrasting patterns of Pliocene and Pleistocene extinctions of marine mollusks in western North and South America. *Geological Society of America, Abstracts with Programs* 33(3):A–35.
- DEVRIES, T. J. 2003. *Acanthina* Fischer von Waldheim, 1807 (Gastropoda: Muricidae), an ocenebrine genus endemic to South America. *The Veliger* 46(4):332–350.
- DEVRIES, T. J. 2005. The Late Cenozoic history of *Xanthochorus* Fischer, 1884 (Gastropoda: Muricidae) in western South America. *The Veliger* 47(4):259–276.
- DEVRIES, T. J. 2006. The Neogene history of *Prisogaster* Mörch, 1850 (Gastropoda: Turbinidae) in South America. *The Nautilus* 120(4):139–149.
- DEVRIES, T. J. 2007. Late Cenozoic tegulines (Gastropoda: Trochidae) from southern Peru. *The Nautilus* 121(4):163–181.
- DEVRIES, T. J. 2008. Pliocene and Pleistocene *Fissurella* Bruguière, 1789 (Gastropoda: Fissurellidae) from southern Peru. *The Veliger* 50(2):129–148.
- DEVRIES, T. J. & D. FRASSINETTI C. 2003. Range extensions and biogeographic implications of Chilean Neogene mollusks found in Peru. *Boletín Del Museo Nacional De Historia Natural (Chile)* 52:141–157.
- DEVRIES, T. J., Y. NARVÁEZ, A. SANFILIPPO, N. MALUMIAN & P. TAPIA. 2006. New microfossil evidence for a late Eocene age of the Otuma Formation (southern Peru). XIII Congreso Peruano de Geología, Lima, Peru, October, 2006. *Sociedad Geológica del Perú, Publicación Especial* 7:615–618.
- DOWSETT, H. J., J. A. BARRON, R. Z. POORE, R. S. THOMPSON, T. M. CRONIN, S. E. ISHMAN & D. A. WILLARD. 1999. Middle Pliocene paleoenvironmental reconstruction: PRISM2. *United States Geological Survey Open File Report*, pp. 99–535.
- ESPOZ, C., D. R. LINDBERG, J. C. CASTILLA & W. B. SIMISON. 2004. Los patelogastrópodos intermareales de Chile y Perú. *Revista Chilena de Historia Natural* 77(2):257–283.
- FILHOL, H. 1880. Mollusques marins vivant sur les côtes de l'Île Campbell. *Comptes Rendues de l'Académie des Sciences de Paris* 91:1094–1095.
- FINLAY, H. J. 1927. A further commentary on New Zealand molluscan systematics. *Transactions of the New Zealand Institute* 57:320–485.
- FUCHIGAMI, T. & T. SASAKI. 2005. The shell structure of the Recent Patellogastropoda. *Paleontological Research* 9(2): 143–168.
- GMELIN, J. F. 1791. *Caroli a Linné, systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Vol. 1(6), 13th Edition. pp. 3021–3910. J.B. Delamollière: Lyon.
- GOLDSTIEN, S. J., N. J. GEMMELL & D. R. SCHIEL. 2006. Molecular phylogenetics and biogeography of the nacellid limpets of New Zealand (Mollusca: Patellogastropoda). *Molecular Phylogenetics and Evolution* 38:261–265.
- HARASEWYCH, M. G. & A. G. MCARTHUR. 2000. A molecular phylogeny of the Patellogastropoda (Mollusca: Gastropoda). *Marine Biology* 137:183–194.
- HEBLING, G. S. 1779. Beiträge zur Kenntnis neuer und seltener Konchylien. Aus einigen Wienerischen Sammlungen. *Abhandlungen einer Privatgesellschaft in Böhmen, zur Aufnahme der Mathematik, der vaterländischen Geschichte, und der Naturgeschichte* 4:102–131.
- HERM, D. 1969. Marines Pliozän und Pleistozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. *Zitteliana* 2:159.
- JONKERS, H. A. 1988. Stratigraphy of Antarctic late Cenozoic pectinid-bearing deposits. *Antarctic Science* 10(2):161–170.
- JONKERS, H. A. & S. P. KELLEY. 1998. A reassessment of the age of the Cockburn Island Formation, northern Antarctic Peninsula, and its palaeoclimatic implications. *Journal of the Geological Society of London* 155:737–740.
- KENSLEY, B. 1972. Pliocene marine invertebrates from Langebaanweg, Cape Province. *Annals of the South African Museum* 60(4):173–190.



- KOUFOPANOU, V. D., G. REID, S. A. RIDGWAY & R. H. THOMAS. 1999. A molecular phylogeny of the patellid limpets (Gastropoda: Patellidae) and its implications for the origins of their antitropical distribution. *Molecular Phylogenetics and Evolution* 11(1):138–156.
- LE ROUX, J. P., S. N. NIELSEN, H. KEMNITZ & A. HENRIQUEZ. 2008. A Pliocene mega-tsunami deposit and associated features in the Ranquil Formation, southern Chile. *Sedimentary Geology* 203:164–180.
- LESSON, R. P. 1830–1831. Voyage autour du monde entrepris par ordre du gouvernement sur la corvette La Coquille pendant les Années 1822–1825. Volume 2 (Zoologie). Arthus Bertrand: Paris. 471 pp.
- LINDBERG, D. R. 1988. The Patellogastropoda. *Malacological Review*, Supplement 4:35–63.
- LINDBERG, D. R. 1998. Order Patellogastropoda. in P. L. Beesley, G. J. B. Ross & A. Wells (eds.), *Mollusca: the southern synthesis. Fauna of Australia* 5:639–652. CSIRO Publishing: Melbourne.
- LINDBERG, D. R. & C. S. HICKMAN. 1986. A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). *Journal of Paleontology* 60(3):661–668.
- LOCARNINI, R. A., A. V. MISHONOV, J. I. ANTONOV, T. P. BOYER & H. E. GARCIA. 2006. *World Ocean Atlas 2005, Volume 1: Temperature*, S. Levitus (ed.), NOAA Atlas NESDIS 61. U.S. Government Printing Office: Washington, D.C. 182 pp.
- LOPEZ, D. A., M. L. GONZALEZ, J. M. URIBE, I. R. RODRIGO & P. A. VERGARA. 1999. Effect of cirripeds on the recruitment of the keyhole limpet *Fissurella picta* (Gmelin). *Ciencias Marinas* 25(1):75–90.
- MACCLINTOCK, C. 1967. Shell structure of patelloid and bellerophonoid gastropods (Mollusca). Peabody Museum of Natural History (Yale University), Bulletin 22:1–140.
- MCLEAN, J. H. 1984. Systematics of *Fissurella* in the Peruvian and Magellanic faunal provinces (Gastropoda: Prosobranchia). *Natural History Museum of Los Angeles County, Contributions in Science* 354:70.
- MENESES, C. I. 1993. Vertical distribution of coralline algae in the rocky intertidal of northern Chile. *Hydrobiologia* 260/261:121–129.
- MORRICONI, E. & J. CALVO. 1993. Influencia ambiental sobre el crecimiento alométrico de la valva en *Nacella* (*Patinigera*) *deaurata* (Gmelin, 1791) del Canal Beagle, Argentina. *Malacologia* 35(1):135–140.
- MUIZON, C. DE. & T. J. DEVRIES. 1985. Geology and paleontology of the Pisco Formation in the area of Sacaco, Peru. *Geologische Rundschau* 74:547–563.
- NAKANO, T. & T. OZAWA. 2007. Worldwide phylogeny of limpets of the order Patellogastropoda: molecular, morphological, and paleontological evidence. *Journal of Molluscan Studies* 73:79–99.
- NIELSEN, S. N. & J. GLODNY. 2006. The middle Miocene climate optimum in central and southern Chile:  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope stratigraphy on warm-water mollusks. XI Congreso Geológico Chileno: Antofagasta, Chile, Actas. Pp. 93–96.
- NOBLE, D. C., E. FARRAR & E. J. COBBING. 1979a. The Nazca Group of south-central Peru: age, source, and regional volcanic and tectonic significance. *Earth and Planetary Science Letters* 45:80–86.
- NOBLE, D. C., E. H. MCKEE & F. MEGARD. 1979b. Early Tertiary “Incaic” tectonism, uplift, and volcanic activity, Andes of central Peru. *Geological Society of America Bulletin* (Part 1) 90:903–907.
- NOBLE, D. C., M. SÉBRIER, F. MEGARD & E. H. MCKEE. 1985. Demonstration of two pulses of Paleogene deformation in the Andes of Peru. *Earth and Planetary Science Letters* 73:345–349.
- NOLAN, C. P. 1991. Size, shape and shell morphology in the Antarctic limpet *Nacella concinna* at Signy Island, South Orkney Islands. *Journal of Molluscan Studies* 57(2):225–238.
- PECHO, V. 1983. Geología de los cuadrangulos de Pausa y Caraveli. Instituto Geológico Minero y Metalúrgico (INGEMMET) Boletín 37:125.
- PETERSEN, G. 1954. Informe preliminar sobre la geología de la faja costanera del departamento de Ica. *Empresa Petroleum Fiscal* 1:33–76.
- PHILIPPI, R. A. 1842–1851. *Abbildungen und beschreibungen neuer oder wenig gekannter Conchylien, unter mithilfe mehrerer deutscher Conchyliologen*. 3 vols. T. Fischer: Kassel.
- PHILIPPI, R. A. 1887. Fósiles terciarios i cuaternarios de Chile. Gobierno de Chile: Santiago. 256 pp.
- POWELL, A. W. B. 1973. The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca* 3(15):75–206.
- RAMIREZ-BÖHME, J. 1996. *Moluscos de Chile*. Vol. I Archaeogastropoda, 2nd edition. Santiago de Chile.
- RAVELO, A. C., D. H. ANDREASON, M. LYLE, A. OLIVAREZ LYLE & M. W. WARA. 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature* 429:263–267.
- RIDGWAY, S. A., D. G. REID, J. D. TAYLOR, G. M. BRANCH & A. N. HODGSON. 1998. A cladistic phylogeny of the family Patellidae. *Philosophical Transactions of the Royal Society, London B* 353:1645–1671.
- RIVERA, R. 1957. Moluscos fósiles de la Formación Paracas, departamento de Ica. *Boletín de la Sociedad Geológica del Perú* 32:165–220.
- SASAKI, T. 1998. Comparative anatomy and phylogeny of the recent Archaeogastropoda (Mollusca: Gastropoda). University Museum, University of Tokyo, Bulletin 38:1–224.
- SCHUMACHER, C. F. 1817. *Essai d'un nouveau système des habitations des vers testacés*. Schultz: Copenhagen. 287 pp.
- SIMPSON, R. D. 1985. Relationship between allometric growth, with respect to shell height, and habitats for two patellid limpets. *Nacella* (*Patinigera*) *macquariensis* Finlay, 1927, and *Cellana tramoserica* (Holton, 1802). *The Veliger* 28(1):18–27.
- SKWARKO, S. K. 1966. Cretaceous stratigraphy and palaeontology of the Northern Territory. Bureau of Mineral Resources, Geology and Geophysics Bulletin 73:133.
- SMITH, E. A. 1877. An account of the petrological, botanical, and zoological collections made in Kerguelen's Land and Rodriguez during the transit of Venus expeditions, carried out by order of Her Majesty's Government in the years 1874–75. *Philosophical Transactions of the Royal Society of London* 168:167–192.
- STILLWELL, J. D. & W. J. ZINSMEISTER. 1992. Molluscan systematics and biostratigraphy. Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. American Geophysical Union, Antarctic Research Series 55:192.
- STREBEL, H. 1907. Beiträge zur Kenntnis der Molluskenfauna der Magalhaen-Provinz. No. 5. *Zoologische Jahrbücher*,

- Abteilung für Systematik, Geographie und Biologie der Tiere 25:79–196.
- STREBEL, H. 1908. Die Gastropoden (mit Ausnahme der nackten Opisthobranchier). Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition (1901–1903) 6(1): 111.
- THIELE, J. 1891. Das Gebiss der Schnecken zur Begründung einer natürlichen Classification. Volume 7(2):249–334, Nicolai: Berlin.
- UBALDI, R. 1985a. A contribution to the knowledge of genus *Nacella* Schumacher, 1817 in the Antarctic and sub-Antarctic regions (Part II). *Argonauta* 1(1):10–12, 17–22.
- UBALDI, R. 1985b. The genus *Nacella* Schumacher, 1817 (Part II). *Argonauta* 1(2–3):29–38.
- VALDOVINOS, C. & M. RÜTH. 2005. Nacellidae limpets of the southern end of South America: taxonomy and distribution. *Revista Chilena de Historia Natural* 78:497–517.
- VÁSQUEZ, J. & J. M. VEGA. 2004. Ecosistemas marinos costeros del Parque Nacional Bosque Fray Jorge. in F. A. Squeo, J. R. Gutiérrez & I. R. Hernández (eds.), *Historia Natural del Parque Nacional Bosque Fray Jorge*. Ediciones Universidad de La Serena: La Serena, Chile. 13:235–252.
- VERMEIJ, G. J. & T. J. DEVRIES. 1997. Taxonomic remarks on Cenozoic pseudolivid gastropods from South America. *The Veliger* 40(1):23–28.
- WATTERS, W. A. & C. A. FLEMING. 1972. Contributions to the Geology and Paleontology of Chiloe Island, Southern Chile, Parts I and II. *Philosophical Transactions of the Royal Society, London* 263:369–408.
- YOON, S. E. & W. KIM. 2007. 18S ribosomal DNA sequences provide insight into the phylogeny of patellogastropod limpets (Mollusca: Gastropoda). *Molecules and Cells* 23(1):64–71.
- ZACHOS, J., M. PAGANI, L. SLOAN, E. THOMAS & K. BILLUPS. 1996. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292(5517):686–693.
- ZINSMEISTER, W. J. 1982. Late Cretaceous-early Tertiary molluscan biogeography of the southern Circum-Pacific. *Journal of Paleontology* 56(1):84–102.

## APPENDIX

Locality-samples. 'GPS' refers to GPS field coordinates; 'GE' refers to coordinates from Google Earth imagery.

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DV 471-1	Highlands of Cerro Poroma, four km east of Pan-American Highway, in bioclastic sandstone and gravel overlying crystalline basement (GE; 14°59'37"S, 74°58'30"W). Late Oligocene.
DV 611a-1	Mid-point of northwestern slopes of Cerro Poroma in bioclastic sandstone and gravel overlying crystalline basement (GE; 14°59'58"S, 74°59'08"W). Late Oligocene.
DV 638-1	Low ridges between Cerro Poroma and Callejon de Piedras, basal bioclastic sandstones above crystalline basement (15°01'53"S, 74°58'52"S). Late Oligocene.
DV 1045-1	Roadcuts along Pan-American Highway near La Planchada (GPS; 16°23'59"S, 73°12'43"W). Pliocene and Pleistocene.
DV 1254-2	Huacllaco, ten km southeast of Chala along Pan-American Highway, about 36–37 meters in measured section (GE; 15°53'16"S, 74°09'59"W). Late early Pliocene.
DV 1254-bal6	Huacllaco, ten km southeast of Chala along Pan-American Highway, 35–35.5 meters in measured section (GE; 15°53'16"S, 74°09'59"W). Late early Pliocene.
DV 1254-10	Huacllaco, ten km southeast of Chala along Pan-American Highway, 47–48 meters in measured section (GE; 15°53'15"S, 74°10'02"W). Early late Pliocene.
DV 1267-1	Roadcuts along Pan-American Highway near La Planchada; 15–20 meters of cross-bedded gravelly sandstone with wavy laminations of ash and scour-and-fill structures (GPS; 16°23'56"S, 73°12'30"W). Pliocene and Pleistocene.
DV 1279-1	Five km west-northwest of village of Ocoña along Pan-American Highway, base of sand-and-gravel quarry, southeast wall, in finely bedded cross-bedded gravel (GPS; 16°25'28"S, 73°09'14"W). Late early Pliocene.
DV 1628-1	Huacllaco, ten km southeast of Chala along Pan-American Highway, bioclastic coquina in lowest five meters of measured section (GE; 15°53'25"S, 74°09'56"W). Late early Pliocene.
DV 1929-1	Huacllaco, ten km southeast of Chala along Pan-American Highway, talus at base of slope on at about 39 meters in measured section (GE; 15°53'15"S, 74°10'01"W). Early late Pliocene.
DV 1941-1	Huacllaco, ten km southeast of Chala along Pan-American Highway, molds in former coquina at 68 m in measured section. (GE; 15°53'02"S, 74°10'07"W). Latest Pliocene.

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